

THE REPRODUCTIVE CYCLE OF THE VIVIPAROUS TELEOST,
NEOTOCA BILINEATA, A MEMBER OF THE FAMILY
GOODEIDAE. IV. THE GERMINAL TISSUE

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INTRODUCTION

The present article is the fourth of a series written by the author on the reproductive cycle of the viviparous cyprinodont, *Neotoca bilineata*. The series has been an attempt to present a more complete study than has been available heretofore on the reproductive cycle of a viviparous teleost. Previous studies by other investigators have been confined largely either to the breeding cycle or to histological descriptions of the ovary, stressing particularly the adaptation of the ovary to the retention of the young during development. Little or no attention had been given to the actual changes in the ovarian soma during gestation until the papers on *Jenynsia (Fitzroyia) lineata* (Hylton Scott, 1928; Siccardi, 1940), *Xiphophorus helleri* (Bailey, 1933), *Neotoca (Skiffia) bilineata* (Turner, 1933), and *Cymatogaster aggregatus* (Turner, 1938b). Some of the above papers were merely introductory descriptions; others were more complete. Furthermore, with the exception of a study of the poeciliids by Turner in 1937, no reference had been made even to the cyclic variation of the germ cells during gestation. Consequently, the writer undertook this investigation with the purpose of presenting in detail an analysis of the reproductive cycle stressing particularly some of the phenomena generally omitted by previous investigators. Articles by the writer on the reproductive cycle of *Neotoca* have described in detail (1) the breeding cycle as observed in the laboratory (1939), (2) the marked cyclic changes in the ovarian soma during gestation (1940), and (3) the variations in the germ cell count during gestation (1941). The present article, the fourth of the series, supplements brief preliminary descriptions (Turner, 1933; Mendoza, 1938) by considering in detail (1) the general description and growth of the germ cells and their follicles, (2) fertilization, (3) the fate of the evacuated follicles, (4) the nature and fate of the atretic follicles, and (5) the origin of germ cells in the adult ovary.

MATERIALS

The present description of the germinal tissue is based on a study of over 30 ovaries in different stages of gestation. The greater part of the material was fixed in Bouin's or Zenker's fluids although fixatives such as Flemming's fluid, osmic acid, and corrosive sublimate were used for special techniques. The principal stains used were iron hematoxylin and Delafield's hematoxylin followed either by Eosin Y or Orange G. In addition, the following special stains were used: Mallory's triple connective tissue stain, Van Geisen's stain, and Foot's modification of Bieschowsky's silver impregnation technique. The customary alcohol-xylol dehydration series was used.

OVARY

The ovary of *Neotoca* is a single, spindle-shaped organ inserted in the median sagittal line; it is attached dorsally to the pleuroperitoneal membrane and ventrally to the mesogaster. The ovary is continuous caudad into a single short gonoduct, a term preferred by Turner and others since, evidently, it is not homologous to the true vertebrate oviduct. *Neotoca* is similar to most viviparous teleosts since almost all possess the single median gonad; only in forms such as *Sebastes rubrovinctus* (Eigenmann, 1892) is the ovary double, and only in few forms such as *Dermogenys pusillus* (Peters, 1865), *Lucifuga subterraneus* and *Stygicola dentata* (Lane, 1903), is the ovary partially fused. So far as is known to the writer, all viviparous teleosts have the single gonoduct even in forms that have the double or partially fused gonads.

GERMINAL TISSUE

Ovigerous folds

The ovary of a teleost may be a solid or hollow organ. In the former case the eggs merely rupture the wall of the gonad, fall into the coelom and then escape to the outside through abdominal pores; in the latter type, the eggs never reach the coelom but make their way out directly from the ovary through the gonoduct. In *Neotoca* the gonad is hollow and the germinal tissue is said to occur internally; the same condition occurs in all other viviparous teleosts known to the writer.

The oöcytes are not scattered at random but are confined to "ovigerous" or egg-bearing folds that are placed on either side of a median sagittal septum.

PLATE I

FIGURE 1. A cross-section of a typical non-gravid ovary (19.5 \times). Part of the ovarian wall at the lower left-hand corner has been removed. In the center of the figure, in a nearly vertical position is the median septum of the ovary. On either side of the septum lie the two ovigerous folds attached by a narrow, constricted stalk to the ovarian wall. The attachment is particularly clear on the left side. The arrow points to the lower edge of the ovigerous fold on the left side. Prominent in the photograph are several developing oöcytes.

FIGURE 2. A growing oöcyte. The photograph shows clearly the nucleolus, the vesicular nucleus, and the early follicle composed of squamous cells.

FIGURE 3. Two good examples of developing oöcytes and their follicles. The medium size oöcyte in the upper portion of the figure shows a nucleus that has lost its vesicular character and has become quite granular. The thickened follicle is the result of rapid mitotic activity that does not cease until the follicle cells become so abundant they form a compact layer of columnar cells as in the egg at the bottom of the figure.

FIGURE 4. A figure that has a two-fold value. First, it shows an oöcyte and its follicle in a stage of development intermediate between that of the two eggs in the preceding figure. The follicle cells now are cuboidal to low columnar and soon will attain the full columnar shape typical of the full grown follicle. Secondly, the figure shows the vacuolated yolk-nucleus (arrow) in a medium size oöcyte. Figures 2 to 4 are intended to show the sequence of changes in the oöcytes and their follicles during growth.

FIGURE 5. A typical delle showing the funnel-like depression of the ovigerous fold epithelium that reaches to the follicle of the egg at the lower left. The intimate contact between the ovigerous fold epithelium and the follicle cells is clearly visible. Within the delle are two spermatozoa (arrows). In the upper left-hand corner is a typical mitotic figure in a growing follicle.

FIGURE 6. A high-power photograph (283 \times) of a follicle after the expulsion of the egg. The position of the former delle is visible still at the upper left-hand corner, showing the place through which the egg escaped from the follicle and the ovigerous fold. The follicle cells still retain their peripheral position although degenerative changes already have started.

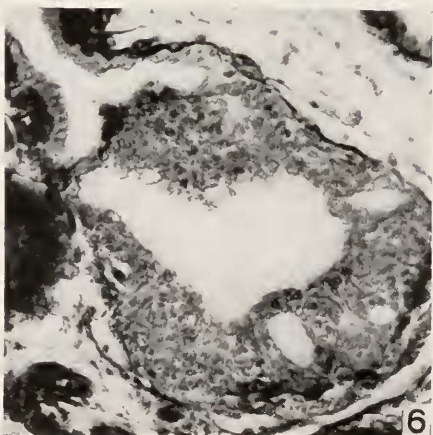
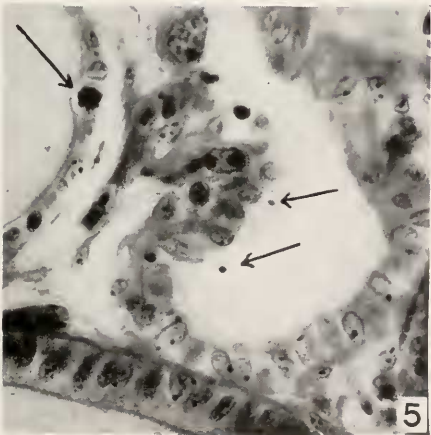
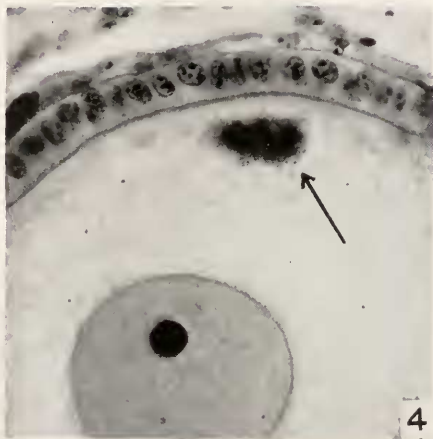
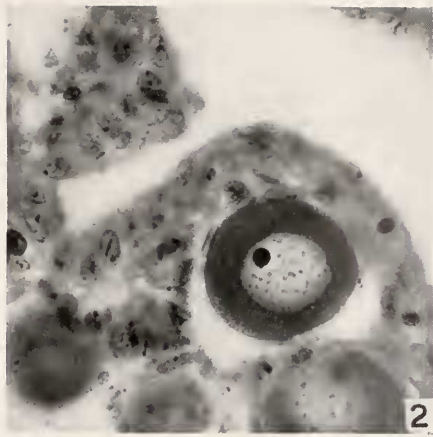


PLATE I¹

¹All figures are contact prints of unretouched photomicrographs. Figure 1 was taken with a Reflex-Korelle camera; all others were taken with a Voigtlander cut-film camera. With exception of Figures 1 and 6, all other photographs were taken with a fluorite, oil-immersion objective and a Hyperplane ocular; the magnification of the oil-immersion photographs is approximately 650 \times .

Each fold is attached by a narrow strip along the dorso-lateral wall of the gonad; the two folds virtually fill the ovarian lumen (Figure 1). Internal ovigerous folds by no means are characteristic of all viviparous teleosts since *Xiphophorus helleri*, *Anableps anableps*, and *Zoarcetes viviparus* are devoid of special folds; the ova merely develop in the walls of the ovary. On the other hand, forms such as *Cymatogaster aggregatus*, *Dermogenys pusillus*, *Jenynsia lineata*, *Sebastes marinus*, etc., resemble Neotoca and other members of the Goodeidae by the presence of one type or another of ovigerous folds or septa. In fact, these folds are so diagnostic in the Goodeidae that Hubbs and Turner (1939) used these same folds, in part, as a basis for their recent taxonomic revision of the family.

Histologically, the folds consist of a loose, collagenous connective tissue that in part shows a marked affinity for argyrophilic stains. A vascular network ramifies throughout the folds and forms a very rich capillary plexus under the epithelium of the folds. It has been shown (Mendoza, 1940) that during gestation, this internal epithelium covering the folds changes from a flattened, indifferent condition to a tall, highly secretory epithelium. Parallel with these changes, the folds likewise become distended with fluid and are invaded by numerous free cellular elements that contribute to the general tumescence of the ovary during gestation. Within the ovigerous folds of Neotoca, the germ cells are evenly distributed throughout the length of the gonad except at the extreme anterior and posterior ends. The growing germ cells are not scattered at random but are normally grouped into clusters of cells that range from minute oöcytes 7 to 10 μ in diameter to fully grown eggs approximately 200 μ in diameter. In addition, these clusters of cells normally occur at the surface of the folds, retaining a very intimate connection with the epithelium (Figures 2, 10, 12), a relationship that was stressed also for *Anableps* by Turner (1938a). At this point of contact between the fully grown ovum and the epithelium, there appears a deep, funnel-like depression of the ovigerous fold epithelium. The cells at the base of the pocket are usually flattened strongly against the follicular cells surrounding the ovum (Figures 5, 9). Normally this depression does not occur at the outer surface of the folds but at the base of one of the many fissures that crease the surface of the folds. This funnel-like depression has been described in other viviparous teleosts and has been identified as a "tubular indentation," a "follicular pore," or a "delle." The two-fold function of this structure will be discussed elsewhere in this paper.

Germ cells and follicles

Germ cells are recognizable when they are but 7 μ in diameter and are undergoing early stages of maturation. Such early cells are grouped into small nests and usually are attached closely to the ovigerous fold epithelium. In these early cells the nucleus is vesicular and occupies fully two-thirds or more of the diameter of the growing oöcyte. The cytoplasm shows an affinity for acidophylic stains and is heavily but evenly granular (Figure 2). The early follicle consists of a few delicate, squamous cells flattened against the surface of the oöcyte (Figure 2); because of the manner of formation of the germ cell nests and the structure of the follicle cells, it is likely that the latter are nothing more than modified fibrocytes of the subepithelial connective tissue.

In the growing oöcyte, furthermore, many changes occur. The nucleus is reduced to one-third of the diameter of the cell and the vesicular character is lost; it becomes granular and even oxyphylic in nature (Figures 2 to 4). During growth, the chromatin loses all affinity for stains although it later reappears in the form of lampbrush chromosomes. Whereas in the early cells the nucleoli may be numerous, less than a micron in diameter and strongly basic in reaction, later they are but few in number, large, vacuolated, and even oxyphylic in their reaction to stains. In general, however, their number, size, and appearance are highly variable in the different cells and at different stages of development. In the growing cells the cytoplasm also undergoes marked changes. The most conspicuous characteristic of the oöcytes is the complete absence of large masses of yolk and the presence of numerous small droplets of oil scattered throughout the granular cytoplasm. The yolk, such as it is, consists largely of a granular, flocculent mass evenly distributed throughout the cytoplasm and very difficult to distinguish except with the use of differential stains and particularly in stages immediately following fertilization. There is not the least similarity to forms such as *Zoarces* in which the yolk appears as large spheres, nor to *Jenynsia* and *Xiphophorus* in which the yolk appears as a large solid mass. Furthermore, another goodeid, *Lernichthys multiradiatus*, shows a heavy yolk mass in the developing embryos, a mass that, though small in size, is so heavy and compact, it cannot in any way be compared to the "yolk" of *Neotoca*. It is regrettable that lack of material prevented further testing or differentiating of fatty and proteinaceous yolk in *Neotoca* although the use of Flemming's fixative on the ova of another goodeid, *Girardinichthys innominatus*, showed beyond doubt that there is a large number of droplets or spheres of fatty yolk concentrated around the nucleus of the ovum. Another conspicuous feature of the fully-developed ovum is a large, vacuolated structure that is very similar to or forms a yolk-nucleus and pallial layer complex (Figure 4). The origin, development, and fate of this yolk-nucleus complex is so interesting in these viviparous forms that it will be discussed at length in a separate paper. It is interesting that, among viviparous teleosts, *Cymatogaster* and *Jenynsia* have yolk nuclei equally as prominent as that of *Neotoca*. The egg membranes of the enlarged oöcytes are not numerous; there is primarily one heavy vitelline membrane densely perforated in part, if not in its entirety, by minute pores. Thus it is similar, though not identical, to the thick, perforated, zona radiata described for *Zoarces* by Stuhlmann and for *Cymatogaster* by Hubbard (1894). Internal to this heavy egg membrane is a more delicate plasma membrane discernible only after fertilization when the heavy outer membrane is separated somewhat from the egg. During growth of the oöcyte, the mitotic activity of the follicle cells not only keeps pace with but actually surpasses the growth of the egg since the follicle changes from a delicate layer of flattened cells to a single, densely-packed row of columnar cells (Figures 2 to 5), a follicle that more closely resembles that of *Xiphophorus* and the early follicle of *Anableps*. In comparison, follicles of a compound nature are found in forms such as *Jenynsia*, *Stygicola*, *Lucifuga*, and *Cymatogaster*. The follicle in *Neotoca* is in turn invested by a thin layer of condensed connective tissue fibers and fibrocytes comparable to the "theca" described by Bailey for *Xiphophorus*. The connective tissue fibers of this "theca" are intimately associated with those of the subepithelial network of the

ovigerous folds and, like reticular fibers, similarly show a marked affinity for argyrophylic stains. Interspersed throughout the interstices of this network there occurs a vascular network more or less prominent in the different follicles and presumably of great importance in the physiological activity of the follicle of the developing oöcyte.

FATE OF THE GERM CELLS

After the ova have attained full growth they suffer one of two fates, either they are fertilized and commence development or they undergo atresia. Both possibilities are considered.

Fertilization

Among viviparous teleosts, fertilization may occur while the egg still is retained within the follicle or after its extrusion into the ovarian lumen. In forms such as *Anableps* and *Xiphophorus*, fertilization occurs within the follicle and the embryo is not released until a short time preceding birth whereas in *Jenynsia*, fertilization is similar but the embryo is discharged early in development. On the other hand, in *Cymatogaster*, *Sebastes marinus* (Williamson, 1910), and *Neotoca*, fertilization and the expulsion of the egg must occur in such rapid succession that it is difficult to separate the two phenomena. Finally, in *Zoarces*, eggs are discharged first into the ovarian lumen and fertilized later. Accompanying these varying conditions of fertilization, structural and functional problems are presented by the different types, problems that are largely beyond the scope of this paper.

Preceding fertilization in *Neotoca*, the different stages of meiosis can be identified readily. Following synzesis which appears in oöcytes 7 to 10 μ in diameter, the chromatin temporarily loses all affinity for stains and later reappears in the form of lampbrush chromosomes. Immediately preceding actual fertilization the chromatin condenses markedly, resembling stages of diakinesis, while the entire germinal vesicle migrates simultaneously toward the periphery of the egg. This migration occurs normally in the direction of the dells, in preparation for the ensuing meiotic divisions and fertilization. Evidently, the meiotic divisions, fertilization, and the expulsion of the egg into the ovarian cavity must occur simultaneously or in very rapid succession, for none of the three phenomena actually have been seen although all stages immediately preceding and following their occurrence have been identified. Unfertilized eggs always have been identified within the follicles; on the other hand, fertilized eggs normally have not been seen within the follicles but always free in the ovarian lumen. The criterion used to distinguish fertilized eggs has been the very radical displacement of cytoplasmic components within the egg and the ensuing segmentation. In these eggs, the cytoplasm is concentrated as a thin peripheral layer, presumably along the animal pole; small oil droplets occur evenly distributed throughout its extent. Underneath the thin blastodisc, the central portion of the fertilized egg is filled by a flocculent, albumen-like substance which apparently replaces the heavy yolk of other viviparous eggs. Occasional spheres of actual yolk can be found, but they are minute and extremely scarce. Although the meiotic divisions

have not been seen, the polar bodies have been identified on the edge of the heavy vitelline membrane. A unique phenomenon is that in the vicinity of the polar bodies the vitelline membrane not only shows a strong affinity for basic stains but also thickens conspicuously at time of fertilization to resemble the typical zona radiata of teleost eggs. Since this thickening of the membrane occurs only in evacuated eggs and only near the polar bodies, it is assumed that it arises in response to the inciting action of the spermatozoa. Due largely to the swelling of the vitelline membrane of these eggs, it can be distinguished from the egg with ease.

It is at the time of fertilization that the delle formed by the ovigerous fold epithelium plays an important role. Through the delle, the spermatozoa actually can approach the egg very closely (Figures 5, 9). If the sperm do, in fact, enter the egg while the latter still is within the follicle, the sperm then must penetrate only through the single row of flattened cells at the base of the delle and the row of columnar follicle cells. However, the writer never has identified an actual pore within the follicular epithelium to permit the entry of the spermatozoa as described for *Xiphophorus* by Bailey. Evidence is available from other viviparous teleosts to show that fertilization within a follicle can and does occur. In *Xiphophorus*, *Anableps*, *Cymatogaster* and *Jenynsia*, eggs are fertilized while still enclosed within the follicle and later are discharged into the ovarian lumen at different stages of development. The second and final function of the delle is that it offers an attenuated and weakened place in the ovigerous fold epithelium through which the egg escapes into the ovarian cavity. A similar role for the delle has been reported for other viviparous teleosts in which it appears.

Upon evacuation of the egg, the follicular cells cease all mitotic activity and suffer one of two or three fates. Sometimes the force of the expulsion of the egg is so great that the follicle cells may be everted part way through the delle. Normally, however, the follicle cells either merely collapse to form a cellular mass of smaller diameter or the follicle cells may retain their peripheral position around the reduced space previously occupied by the egg (Figure 6). Despite these differences in evacuated follicles, the cells eventually lose their regularity and become a disorganized mass of cells. The evacuated follicle does not assume the "windswept appearance" of the *Xiphophorus* follicle (Bailey) nor does it become hypertrophied as in *Sebastes marinus* and *Anableps anableps*. It is impossible to compare the spent follicles of *Neotoca* with the mammalian corpora lutea since in *Neotoca* there is no evidence of a pronounced physiological activity; actually, the follicle cells are small and shrunken. Pycnotic figures of degeneration make their appearance soon after the extrusion of the egg; vacuolization and fatty degeneration have been found among these follicles (Figure 6). By the time embryos are 1.5 mm. in length it is difficult to distinguish between spent follicles and ordinary atretic follicles. It is to be expected, perhaps, that in *Neotoca* the follicle should be passive and soon degenerate for, since the embryo develops completely within the ovarian lumen, the follicle is relieved of all responsibility of serving the developing embryo in a nutritive or respiratory capacity. Thus the *Neotoca* follicle is not taxed with a physiological burden similar to that of *Anableps* nor poeciliids like *Xiphophorus* in which the embryo develops completely within the follicular sac.

Atresia of the eggs and follicles

Egg degeneration is found in all ovaries. It is evident that eggs degenerate rapidly if not fertilized soon after they have attained full growth. As many as 25 eggs in various stages of atresia have been found in a single non-gravid ovary. In typical cases of degeneration which occur during all stages of gestation, both the follicle and the egg are involved. Normally, the egg and especially the cytoplasm is the first to disintegrate; the alveolar structure is lost and frequently the cytoplasmic residue coagulates upon fixation. Coexistent with these changes, the follicle cells lose their regularity, mitosis ceases, the vitelline membrane is thrown into folds, and the follicle cells are displaced toward the atretic egg. Normally, however, the follicle cells retain their peripheral position for some time while the cytoplasm of the egg breaks up. It is likely that the debris of the egg is removed in part by absorption and in part by actual phagocytosis. With the removal of most of the cytoplasmic residue, the follicle collapses completely and forms a nearly solid group of cells surrounding a mass of debris (Figures 7, 8). During this process, slight lymphocyte infiltration usually occurs and may be instrumental in aiding the process of disintegration. In the follicle cells, the nuclei are the first to undergo pycnotic degeneration; the breakdown occurs gradually, cell by cell. The degeneration picture most definitely is not one of complete breakdown of all or most cells at once. In a few isolated cases an abnormally heavy lymphocyte infiltration may occur and in others the follicle may precede the egg in degeneration. These, however, are infrequent in their occurrence. Eventually, regardless of the method of atresia, the end result is the removal of the degenerating mass of cells from the stroma of the ovary.

ORIGIN OF THE GERM CELLS

Although no study has been made of the origin of germ cells in the embryonic gonad, the writer feels that there is available interesting evidence on the origin of the cells in the adult gonad. The observation has been made repeatedly that

PLATE II

FIGURE 7. An atretic follicle showing the disorganized state of the follicle cells, the cellular debris, some fatty degeneration, and several large vacuoles that have appeared between the cells.

FIGURE 8. A degenerating follicle that has been reduced to a small cellular mass. In the center there occurs some cellular debris and one atretic cell (arrow).

FIGURE 9. This and the remaining figures on the plate have the single purpose of showing the frequent occurrence of growing oöcytes in the ovigerous fold epithelium and the possible origin of some germ cell nests from the epithelium. The arrows indicate clearly an oöcyte in the epithelium that lines the delle and three spermatozoa within the delle proper. This and Figure 5 show the relation of the ovigerous fold epithelium of the delle to the egg and its follicle.

FIGURE 10. The arrows indicate first, a developing oöcyte in the ovigerous fold epithelium and second, a new germ cell nest apparently derived from the epithelium.

FIGURE 11. A single, distinct oöcyte in the epithelium of the ovigerous folds. The sub-epithelial connective tissue, showing black in the photograph, indicates clearly that the germ cell is in the epithelium and not merely lying against it.

FIGURE 12. The opening that shows in the center of the photograph is a cross-section of a delle. The arrows indicate two oöcytes within the epithelium of the delle and other germ cells that apparently have broken through the subepithelial connective tissue fibers to form a small clump or nest of growing oöcytes. The photograph shows clearly how the basement membrane has been ruptured completely at this point, indicating a complete continuity between the growing oöcytes and the ovigerous fold epithelium.

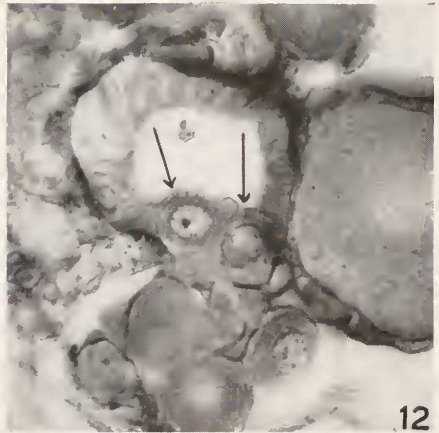
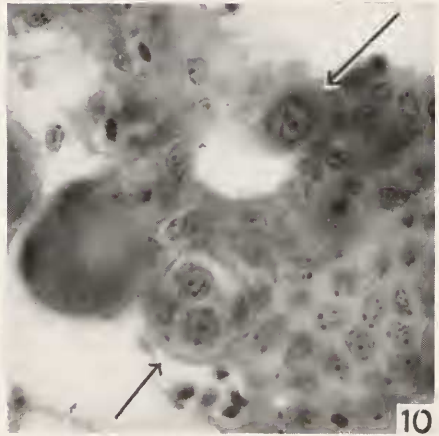
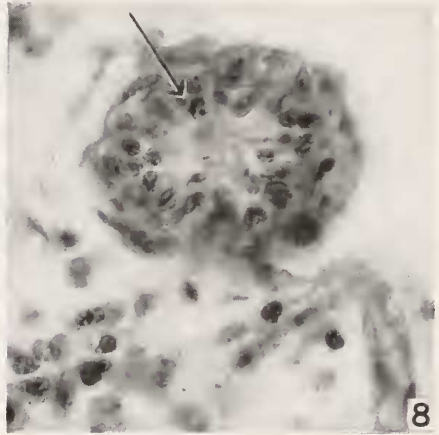
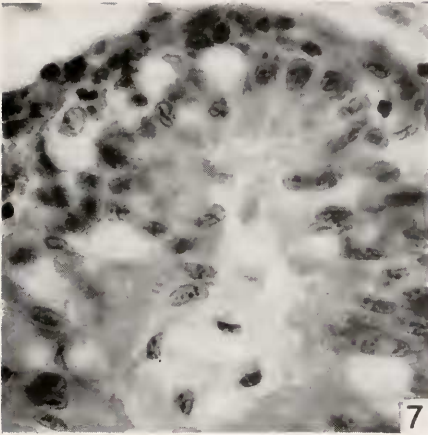


PLATE II ²

² See footnote 1.

cells normally occur in clusters at the surface of the ovigerous folds (Figures 2, 10, 12). This is true particularly at the interlobular fissures that occur in the ovigerous folds. The attachment of the full grown oöcytes to the ovarian delle has been described in another part of this paper. Histologically, it is evident that the subepithelial connective tissue fibers are in direct continuity with those surrounding the large individual cells and clusters of small cells (Figure 10). Furthermore, there are frequent examples of prominent invaginations of the ovigerous fold epithelium to form small nests or clusters of epithelial cells. These invaginated nests to all purposes appear like clusters of typical gonial cells (Figures 10, 12). In addition, typical growing oöcytes frequently appear in these invaginated cell nests (Figure 12). The striking feature of many of the nests is that the cells still are in direct continuity with the epithelial cells on the surface of the ovigerous fold; in other words, the invaginated cluster of cells has not been pinched off as yet from the superficial epithelium. With differential stains, it is possible to determine that the invagination of the cells does not always break through the underlying, subepithelial connective tissue fibers but rather that the heavy fibers and the accompanying fibrocytes are carried along with the invagination to form a thin connective tissue sheath around the nest of cells. Thus, in these cases, not only the cells within the nests but also the connective tissue fibers around the nests are continuous with the corresponding elements at the surface of the ovigerous folds. These nests then are pinched off from the surface. Lastly, the observation has been made frequently that oöcytes may occur within the epithelium proper of the ovigerous folds. They are much larger than the adjacent epithelial cells and have the customary large vesicular nucleus (Figures 9 to 12). A secondary migration of these oöcytes into the epithelium appears unlikely. Rather, it appears that these are examples of epithelial cells differentiating *in situ* to form germ cells. In these cases, differentiation occurs without the usual invagination. Therefore, in view of (1) the intimate histological connection between the oöcytes and the ovigerous fold epithelium, (2) the actual invagination of the epithelial cells, and (3) the occurrence of typical oöcytes in the epithelium proper, the writer is firmly convinced that, in the adult gonad at least, some of the germ cells arise from the ovarian epithelium on the ovigerous folds. It is interesting that Turner made similar observations in the ovary of *Anableps anableps*. He not only stressed the subepithelial position of the germ cell nests and oöcytes but also noted occasionally single oöcytes in the epithelium itself. However, he arrived at no conclusions regarding the origin of the germ cells.

SUMMARY

1. Two ovigerous folds, one on either side of the median sagittal septum of the ovary are described as bearing the germ cells.
2. Oöcytes normally occur in clusters at the surface of the ovigerous folds.
3. Follicular pores or delles not only facilitate access of the spermatozoa to the ovum but also provide a place for the escape of the fertilized egg.
4. The growing oöcyte is characterized largely by the absence of large masses of yolk and the presence of numerous oil droplets. During growth the nucleus changes from a typical germinal vesicle to a granular, eosinophilic body in which the chromatin exhibits only a weak affinity for stains.

5. The follicle of *Neotoca* changes during growth from a tenuous layer of scattered squamous cells to a thick, simple layer of columnar cells.
6. Fertilization, the completion of the meiotic divisions, and the escape of the egg are described as occurring simultaneously or in extremely rapid succession.
7. Normally evacuated follicles cannot be compared in any way to the mammalian corpus luteum.
8. In the atresia of the follicles the following phenomena are believed to occur: some fatty degeneration, some liquefaction or vacuolization of cells, some lymphocyte infiltration, some phagocytosis, and lastly, some absorption by the surrounding cells.
9. Some, if not most, of the germ cells of the adult gonad of the female are believed to arise from the epithelium of the ovigerous folds.

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